DR. MARTIN ANDRES NUÑEZ (Orcid ID : 0000-0003-0324-5479)

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Highly invasive tree species are more dependent on mutualisms

Jaime Moyano[1], Mariano A. Rodriguez-Cabal[1-2], Martin A. Nuñez[1]

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Authors affiliation:

[1] Grupo de Ecología de Invasiones, INIBIOMA, CONICET, Universidad Nacional del Comahue, Quintral 1250, San Carlos de Bariloche, CP 8400, Argentina

[2] Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, Vermont, 05405 USA

Corresponding author:

Name: Martin A. Nuñez

Address: Quintral 1250, San Carlos de Bariloche, CP 8400, Argentina

Phone number: +54 9 294 457 0021

Email address: nunezm@gmail.com

Abstract

Why some species become invasive while others do not remains an elusive question. It has been proposed that invasive species should depend less on mutualisms, because their spread would then be less constrained by the availability of mutualistic partners. We tested this idea with the genus *Pinus*, whose degree of invasiveness is known at the species level (being highly and negatively correlated with seed size) and which forms obligate mutualistic associations with ectomycorrhizal fungi (EMF). Mycorrhizal dependence is defined as the degree to which a plant needs the mycorrhizal fungi to show the maximum growth. In this regard, we use plant growth response to mycorrhizal fungi as a proxy for mycorrhizal dependence. We assessed the responsiveness of *Pinus* species to EMF using 1206 contrasts published on 34 species, and matched these data with data on *Pinus* species invasiveness. Surprisingly, we found that species which are more invasive depend more on mutualisms (EMF). Seedling growth of species with smaller seeds benefited more from mutualisms, indicating a higher dependence. A higher reliance on EMF could be part of a strategy in which small-seeded species produce more seeds that can disperse further, and these species are likely to establish only if facilitated by mycorrhizal fungi. On the contrary, big seeded species showed a lower dependence on EMF, which may be explained by their tolerance to stressful conditions during establishment. However, the limited dispersal of larger seeds may limit the spread of these species.

We present strong evidence against a venerable belief in ecology that species that rely more on mutualisms are less prone to invade, and suggest that in certain circumstances greater reliance on mutualists can increase spread capacity.

Keywords: mycorrhiza, facilitation, mutualists, Pinus, plant invasions, seed size, seedling growth.

Introduction

Predicting what species are more likely to invade when introduced to a new region represents a major challenge in modern ecology. However, understanding why some plant species become invasive while others do not remains elusive (van Kleunen et al. 2015, Seebens et al. 2016). The "ideal weed" hypothesis posits that invasive plant species should depend less on mutualistic interactions (Baker 1965). Several studies have suggested that plant species that rely more on mutualisms are less prone to invade (Richardson et al. 2000). Therefore, plant species that rely more on pollinators (Burns et al. 2011, Pyšek et al. 2011, Rodger et al. 2013, Razanajatovo et al. 2016), on seed dispersers (Richardson et al. 2000) and on mycorrhizal associations (Vogelsang et al. 2004, Vogelsang and Bever 2009) are proposed to be less invasive.

Dependence on mutualists may affect the success of plant invasions in different ways. There may be no dependence between plants and mutualists, in which case those plants should be more likely to be invasive because their spread is not limited by the presence of mutualists (Baker 1965, Rodger et al. 2013). For example, the highly invasive *Atriplex* spp. and *Hakea* spp. in South Africa (Henderson 2007) and *Brassica* spp. in North America (Oduor et al. 2015) are non-mycorrhizal plants (Traveset and Richardson 2014). Also many successful invasive plants are self-pollinated, including *Alliaria petiolata, Bromus tectorum, Carpobrotus edulis, Hypericum perforatum,* and *Mesembryanthemum crystallinum* (Richardson et al. 2000). Some plants may depend facultatively on mutualisms, so they can still establish and invade in the absence of their mutualistic partners (Traveset and Richardson 2014). For example, 90% of woody invasive plants do not depend exclusively on animal dispersers (Traveset and Richardson 2014). Finally, some plants are highly dependent on

mutualisms and will invade only in the presence of their mutualists (Richardson et al. 2000). For example, out of 60 *Ficus* species introduced to Florida only 3 have become invasive, and only after the introduction of their highly specific pollinator wasps (Ramírez 1988, McKey and Kaufmann 1991, Nadel et al. 1992). While many studies have supported this general pattern of higher likelihood of becoming invasive for plant species with lower dependence on mutualisms using isolated examples, no study has quantified yet the dependence on mutualisms along a gradient of plant invasiveness.

The genus *Pinus* is an ideal study system to evaluate the dependence of invasive plants on mutualisms. Many species of this genus have been widely planted around the world, some of which have become invasive and others have not (Simberloff et al. 2010, Richardson and Rejmánek 2011, Nuñez et al. 2017). Also, invasions by *Pinus* have been intensively studied (Richardson 2006), and a score was developed to quantify invasiveness among different pine species (Z score) (Rejmánek et al. 2005; see also Rejmánek and Richardson 1996). Further, *Pinus* species form obligate and highly specific mutualistic interactions with ectomycorrhizal fungi (EMF) (Mikola 1970, Koele et al. 2012), which is the mycorrhizal association of 60% of the trees on the world (Steidinger et al. 2019). The degree to which *Pinus* species need ectomycorrhizal fungi to produce the maximum growth is defined as mycorrhizal dependence (Gerdemann 1975, Janos 2007). In this regard, *Pinus* growth response to ectomycorrhizal fungi can be used as a proxy for mycorrhizal dependence (Menge et al 1978, Plenchette et al. 1983, Tawaraya 2003, Moora 2014). Additionally, working with species within the same genus minimizes confounding effects arising from phylogenetic relatedness. Here we focus on the seedling stage because: (1) *Pinus* species vary greatly in their growth response to EMF at the seedling stage (Karst et al. 2018), (2) it is the most vulnerable stage in the life cycle of a plant (Harper 1977, Baskin and Baskin 1998, Fenner and Thompson 2005), and (3) patterns of growth at the seedling stage are very good predictors of patterns of growth at maturity for woody species (Cornelissen et al. 1998).

Here, we test the hypothesis that *Pinus* species with higher invasiveness depend less on the mutualisms with EMF. We define invasiveness here as the potential of a species to increase in abundance and/or distribution when introduced to a new region (Pyšek and Richardson 2007). To test this hypothesis we compiled a database of 1206 contrasts on 34 *Pinus* species that evaluated the growth of seedlings, with or without EMF inoculation (i.e. mycorrhizal responsiveness). Using linear

models we evaluated the relationship between *Pinus* species invasiveness as scored by Rejmánek et al. (2005) and the response of seedling growth to EMF inoculation. Seed mass is among the plant traits with more evidence showing a correlation with plant invasiveness (Rejmánek 2000, Hamilton et al. 2005, Moravcová et al. 2010, Pyšek et al. 2015, Novoa et al. 2016). To further understand the relationship between invasiveness and mutualist dependence we evaluated the relationship between seed mass and the effect of EMF on seedling growth.

Methods

We quantified *Pinus* species responsiveness to mycorrhizas (Janos 2007, Smith et al. 2009) following the method in Veresoglou et al. (2018): comparing the growth of *Pinus* seedlings with and without EMF. Although species response to mycorrhizas is evaluated under highly controlled conditions, this response could be used as a proxy for plant mycorrhizal dependence (Gerdemann 1975, Menge et al 1978, Plenchette et al. 1983, Tawaraya 2003, Moora 2014). For this purpose we used data from published studies to perform a meta-analysis conforming to PRISMA guidelines (Moher et al. 2009)

We built our database of published studies starting with a global database of plant response to mycorrhizal fungi (MycoDB), which contains studies where plants were grown either with mycorrhizal fungi or without them and the resulting plant growth was measured (Chaudhary et al. 2016). MycoDB contains 444 contrasts from 58 papers focused on *Pinus* species (Fig. S1). On March 2019 we conducted a literature search of the Scopus database using the keywords "pinus" OR "pine*" AND "inocul*" AND "mycorrhiz*" OR "ecotmyc*". We evaluated the results obtained with this search and the references therein to identify 112 papers which met the following requirements: (1) comparison of *Pinus* seedling biomass measured after growing with or without inoculation of EMF and, (2) the study was not included in MycoDB. Those articles that did not include control treatments (without EMF inoculation) were not included, since comparisons were not possible. For each study we obtained information on seedling biomass with and without inoculation of EMF. When they were available, we extracted data from whole plant biomass (shoot + root), and if such data were unavailable we tallied only shoot biomass. If an experiment contained the manipulation of a factor apart from fungal inoculation (e.g., substrate fertilization, age of seedlings at moment inoculation), the

results were included in our database as separate contrasts within the same experiment, following the same criteria as the authors of MycoDB (Chaudhary et al. 2016).

We also extracted, from each experiment, data on co-variables that we expected to influence *Pinus* seedlings response to EMF: (1) whether the experiment was performed in the field or under controlled conditions (greenhouse or growth chamber), (2) the duration of the experiment, (3) whether the substrate was fertilized or not, (4) whether *Pinus* seedlings were inoculated with a single fungal species or with multiple fungal species, (5) the age of the *Pinus* seedlings when inoculated and, (6) whether the experiment took place in the native or in the introduced range of the *Pinus* species. We digitized data available in graphs using Web Plot Digitizer 4.1 (Rohatgi 2018). In combination with previous contrasts from MycoDB, the final database we obtained consists of 1206 contrasts from 170 papers. Of these, 346 contrasts were carried out in the field and 860 took place under controlled conditions (either in a greenhouse or a growth chamber).

We calculated an effect size (ES) for each study using log response ratio as:

$$(1)\quad ES = \ln (EMF_P/EMF_A)$$

where EMF_P is the biomass of seedlings in the presence of EMF and EMF_A is the biomass of seedlings in the absence of EMF. We calculated a mean effect size for each *Pinus* species using an unweighted average of all the contrasts for each species, following Karst et al. (2018). A positive effect size indicates that *Pinus* seedlings benefit from the presence of EMF, whereas if the effect size is negative seedlings are negatively affected by EMF. Also, the absolute value of the effect size is an indicator of the magnitude of the response of the seedlings to the presence of EMF, whether positive or negative. Therefore, some *Pinus* seedlings may have a strong response while others may have a weak response even when in both cases seedlings benefit from EMF inoculation (i.e. both responses are positive).

For each *Pinus* species included in the database (Appendix S1: Table S1) we obtained information on life-history traits from different sources (Committee-for-Compilation-of-Chinese-Tree-Species-Manuals 1978, Grotkopp et al. 2004, Krugman and Jenkinson 2008, Zhao et al. 2011, McGregor et al. 2012, Yang et al. 2018). We were interested in the different traits that were found to

predict invasiveness (seed mass, juvenile period, and interval between large seed crops) and were therefore used to calculate an invasion index (i.e. the Z score) (Rejmánek et al. 2005; see also Rejmánek and Richardson 1996). The Z score is calculated for each *Pinus* species as follows:

$$(2)\ Z\ score = 23.39 - 0.63 * \sqrt{SM} - 3.88\sqrt{JP} - 1.09 * SC$$

Where SM is seed mass, JP is juvenile period and SC is the interval between large seed crops for each *Pinus* species. A species with negative Z score would be considered non-invasive while a species with positive Z score would be considered invasive. For example, according to a global database of invasive trees and shrubs, 90 % of *Pinus* species that have become invasive around the world have a positive Z score (Rejmánek and Richardson 2013). Also the higher the value of positive Z scores the more invasive a species would be (Rejmánek et al. 2005). In this regard, based on a recently compiled database of worldwide occurrences of naturalized *Pinus* species (Perret et al. 2019) the Z score is positively and highly correlated with the number of naturalized occurrences for the 34 species included in our database ($p < 0.0001$; $R^2 = 0.38$). On the other hand, lower values of seed mass correspond to a higher invasive capacity for *Pinus* species (Richardson et al. 1990, Richardson et al. 1994, Rejmánek 1996, Rejmánek and Richardson 1996, Grotkopp et al. 2002, Grotkopp et al. 2004, Rejmánek et al. 2005). We also extracted data on seed wing length from (McGregor et al. 2012) to obtain the ratio between seed mass and seed wing length, defined as seed wing loading index (Richardson et al. 1990). This trait is a good indicator of how effectively the seed can be dispersed by wind and, therefore, it may help understand why some *Pinus* species spread more rapidly (Richardson et al 1990, Rejmánek 1996).

To quantify the importance of *Pinus* species invasiveness (using either Z score or seed mass as a proxy) and other co-variables as the potential drivers of the effect of EMF on seedling growth, we used linear regression models (lm function) (Wilkinson and Rogers 1973, Chambers et al. 1990). Further, to evaluate the relationship between *Pinus* species dispersal ability and seedling responsiveness to EMF we used seed loading index as a predictor variable (an alternative to species invasiveness), together with other co-variables. We tested the independence of all predictor variables through multicollinearity, using the variance inflation factor (VIF) (VIF function) (Fox and S. 2010). None of the variables showed multicollinearity (all VIF values were below 2), so we incorporated all of them in our models. However, it is important to make clear that we never included Z score, seed

mass or seed loading index on the same model since Z scores and seed loading indexes are calculated based on seed mass. We tested our models for normality by visually analyzing the distribution of each model´s residuals (Appendix S2: Fig. S1a & S2a). We evaluated the homogeneity of variance checking the absence of patterns between model residuals and fitted values (Quinn and Keough 2002) (Appendix S2: Fig. S1b & S2b). Further, none of the data points in our dataset showed a Cook´s distance over 1, indicating the absence of influential cases (Cook and Weisberg 1982) (Appendix S2: Fig. S1c & S2c).

To test if there is a phylogenetic signal in our response variable we used the phylogenetic tree constructed by McGregor (2012) and estimated Abouheif´s C_{mean} (Abouheif 1999, Pavoine et al. 2008) (abouheif.moran function from package adephylo) (Jombart and Dray 2008). To evaluate if there is a publication bias in our database we used a nonparametric rank correlation test, Spearman's rho, a powerful test for analyses including more than 75 contrasts (Begg and Mazumdar 1994). According to this test a significant correlation between effect size and sample size would indicate bias in publication. We also built a funnel plot to observe how the distribution of effect sizes changes with the sample size. Finally, we included sample size (i.e. number of replicates) of each contrast as a predictive variable in the multiple regression models to account for a possible publication bias. We performed all statistical analyses using R software v.3.5.1 (R Core Team 2019).

Results

The effect of EMF inoculation on *Pinus* seedling growth increased with increasing *Pinus* invasiveness ($R^2 = 0.37$; $p = 0.0001$; Fig. 1a) and decreased with increasing seed mass ($R^2 = 0.24$; $p = 0.0030$; Fig. 1b). Even without considering the four species with clearly negative Z scores, species with higher invasiveness showed higher growth response to EMF ($R^2 = 0.16$; $p = 0.0288$; Appendix S2: Fig. S3). This growth response ranged from nearly 0% for big seeded species with low invasiveness to nearly 100% biomass increase for small seeded species with high invasiveness. Seedling growth response to EMF decreased with seed wing loading ($R^2 = 0.20$; $p = 0.0072$; Appendix S2: Fig. S4). Even when removing data from the *Pinus* species with extreme values of this trait, species dependence to EMF still decreased with higher seed wing loading ($R^2 = 0.16$; $p = 0.0244$; Appendix S2: Fig. S5).

When accounting for experiment conditions (field experiment or under controlled conditions, experiment duration, fertilization, single fungal species or multiple fungal species inoculation, the age of seedlings when inoculated and the location of the experiment in the native or introduced range of the *Pinus* species) we found a significant effect of many co-variables. Seedling response to EMF increased with the duration of the experiment (Appendix S2: Fig. S6) and with inoculation of multiple fungal species (Appendix S2: Fig. S8). On the other hand, species mycorrhizal responsiveness decreased with soil fertilization (Appendix S2: Fig. S7) and seedling age at the moment of inoculation (Appendix S2: Fig. S9). However, seedling growth response was not affected by whether the experiment was carried out under controlled conditions or in the field (Appendix S3: Table S1). Finally, the effect of the location of the experiment in the native or the introduced range of *Pinus* species on seedling growth response to EMF showed inconclusive results (Appendix S3: Table S1). When using the Z score as proxy for *Pinus* species invasiveness we found that seedling response to EMF increased in the native range (Apprendix S3: Table S1a). However, when using either seed mass or seed wing loading index as proxy for *Pinus* species invasiveness we found no significant effect of experiment location (Appendix S3: Table S1b & S1c).

After accounting for experimental conditions the effect of EMF on *Pinus* seedling growth still increased with *Pinus* invasiveness ($p < 0.0001$; Appendix S3: Table S1a), and decreased with *Pinus* seed mass ($p = 0.0021$; Appendix S3: Table S1b) and *Pinus* seed wing loading ($p = 0.0068$, Appendix S3: Table S1c). Therefore, across many different scenarios and context conditions the traits that favor *Pinus* invasiveness and seed dispersal remained strong drivers of their response to EMF: *Pinus* species that can disperse further and are more invasive have higher responsiveness to EMF. We found no evidence that the effect of EMF on seedling growth is affected by species relatedness (Abouheif´s $C_{mean} = 0.116$, $p = 0.159$) (Münkemüller *et al.* 2012). On the other hand, we found evidence for publication bias in our database (Spearman's rho = -0.13; $p < 0.0001$), given by an overrepresentation of positive effect sizes at low sample sizes (Appendix S4: Fig. S1). However, when including the sample size as a predictive variable in our models, to account for this publication bias, our results were unchanged (Appendix S5: Table S1).

Discussion

Contrary to theoretical predictions, our results show that *Pinus* species which are more invasive depend more on mutualistic partners. Ectomycorrhizal fungi (EMF) generated a bigger increase of seedling growth for *Pinus* species that are more invasive (higher Z score and lower seed mass). The interaction between plants and mycorrhizal fungi benefits the plants, in terms of increased water and nutrient absorption, but also has its costs, in terms of a proportion of carbon assimilation destined to the fungi and not to plant growth (Johnson et al. 1997, Johnson and Graham 2013). One possibility is that the balance between the benefits and costs of this mutualism differs between *Pinus* species differing in seed mass. Larger seeds tend to have higher levels of reserves and to produce larger seedlings, which usually have deeper roots, increasing water and nutrient absorption without the need of symbionts (Harper et al. 1970, Baker 1972, Buckley 1982, Gross 1984, Stock et al. 1990, Jakobsson and Eriksson 2000). As a consequence, these seedlings may be less limited by root absorption and less benefited by EMF. *Pinus* species are obligate mycorrhizal plants (Koele et al 2012) and as such require associations with appropriate fungi to survive (Smith and Read 2008, Brundrett and Tedersoo 2018). However, our results suggest that big seeded species may persist for long periods of time in areas with low mycorrhizal inoculum, since their seedlings may survive longer awaiting mycorrhizal fungi.

Relying more on EMF could be a mechanism that helps explain why small-seeded *Pinus* species are more invasive. Seed size is probably the trait with more evidence showing a correlation with plant invasiveness: smaller seeded species are more invasive (Rejmánek 2000, Hamilton et al. 2005, Moravcová et al. 2010, Pyšek et al. 2015). According to the seed size - seed number trade-off, species may produce either many small seeds or a few large seeds (Jakobsson and Eriksson 2000, Henery and Westoby 2001, Moles and Westoby 2006). Species with small seeds tend to have higher fecundity (seeds produced per adult per year), part of a strategy aimed to produce enough propagules to ensure that at least some seeds will find suitable microsites for seedling growth (Jakobsson and Eriksson 2000). Smaller seeds tend to produce smaller seedlings, which are more susceptible to stressful conditions, such as low water availability and low nutrient levels (Baker 1972, Buckley 1982, Leishman and Westoby 1994, Moles and Westoby 2004). However, facilitated by the mutualism with EMF these seedlings may be more capable to survive and grow under these stressful

conditions (Rapparini and Peñuelas 2014). Thus, the strategy of producing more seeds and associating with EMF would promote the establishment of a higher number of seedlings than that of species that produce larger (and fewer) seeds.

The dispersal ability of a plant may also be related to its dependence on the mutualism with mycorrhizas. A recent meta-analysis showed that adaptations for long-distance dispersal are more frequent in mycorrhizal plants than in non-mycorrhizal plants (Correia et al. 2018). In our study, the dependence of *Pinus* species on EMF showed a gradient, from highly dependent on EMF (small-seeded species with low seed wing loading) to low dependence (large-seeded species with high seed wing loading). This gradient may be associated with the dispersal ability of *Pinus* species differing in seed wing loading, where small-seeded species with relatively big seed wings disperse further, by means of wind, than large-seeded species with relatively small seed wings (Greene and Johnson 1993, Groom 2010, Zhu et al. 2015). The dispersal ability of different *Pinus* species may have an influence on their invasiveness, limiting the spread of large seeded species with relatively small seed wings (Rejmánek 1996). For example, *Pinus pinea*, one of the species with the largest seed wing loading in the genus, was introduced in ~1750 in South Africa but never became invasive (van Wilgen and Richardson 2012), possibly because seed dispersal was highly limited and seedlings were only found in the understory of plantations (van Wilgen and Siegfried 1986). Our study shows that species that spread further depend more on EMF. This is contrary to what we expected, because the availability of suitable mycorrhizal partners decreases with distance from the parent tree (Collier and Bidartondo 2009, Nuñez et al. 2009, Hayward et al. 2015, Horton 2017). However, where appropriate biotic vectors increase mycorrhizal dispersal, availability of EMF inoculum may not limit the distance for *Pinus* establishment (Nuñez et al. 2013, Wood et al. 2015). In this context, the positive association between seed dispersal and dependence on EMF may be advantageous for expanding the range of the plant population (Correia et al. 2018). Also, the ability to disperse further may reduce competition between seedlings and with the mother plant, increasing the probability of survival for each individual seedling, and therefore contributing to population growth (Law et al. 2003) and rapid expansion (Clark et al. 2001).

In accordance with previous studies, our results show that *Pinus* seedling growth response to EMF increased with experiment duration (Lekberg et al. 2018) and inoculation of multiple fungal

species (Perry et al. 1989, Dalong et al 2011). On the other hand, species mycorrhizal responsiveness decreased with soil fertilization (Browining & Whitney 1992, Diaz et al. 2010) and age of the seedlings when inoculated. We found no conclusive results regarding species responsiveness to EMF inoculation in the native range compared to the introduced range. In this regard, we found no evidence of reduced mycorrhizal dependence in *Pinus* introduced range (Pringle et al. 2009, Seifert et al. 2009)

Proxies for species invasiveness are very useful but none of them are expected to predict all successful and failed invasions. Many factors are involved in biological invasions, which make them extremely difficult to anticipate (van Kleunen et al. 2015, Seebens et al. 2016). In the case of *Pinus* some of the drivers of invasions are not related to species invasiveness, but to biogeographic or human factors (Essl et al. 2010, McGregor et al. 2012). Nevertheless, invasive traits have shown to be good predictors of invasion success. For example, all *Pinus* species with positive Z score (i.e. classified as invasive) that have been introduced to new regions have become invasive outside their native range (Grotkopp et al. 2004). Further, according to a global database of invasive trees and shrubs, 90% of *Pinus* species that have become invasive around the world have been classified as invasive according to the Z score (Rejmánek and Richardson 2013). In addition, according to a recently compiled database of *Pinus* species naturalized occurrences, the Z score is highly and positively correlated with the number of sites where each species has become naturalized ($p < 0.0001$; $R^2 = 0.38$) (Perret et al. 2019). However, some of the *Pinus* species regarded as non-invasive have not been widely introduced outside their native range (Essl et al. 2010, McGregor et al. 2012), which results in reduced number of opportunities for invasion (Lockwood et al. 2005). We acknowledge that this proxy of *Pinus* invasiveness is not a perfect predictor of invasion success, but we consider it a useful indicator of how likely is a species to become invasive when introduced to a new region.

Our results show that *Pinus* species that are more invasive respond more to the mutualism with EMF, and this pattern may remain consistent across other taxa. For instance, the same pattern of decreasing responsiveness to mycorrhizas with increasing seed mass was found for species belonging to many different plant families in a tropical forest (Janos 1980), for species of the Ericaceae family (Allsopp & Stock 1992) and for species of the Rosidae subclass (Allsopp & Stock 1995). On the other hand, Reinhart et al. (2017) found no evidence that plant invasiveness was associated with mycorrhizal responsiveness for the Poaceae and Asteraceae families. Further, the results we have

showed here may have implications not only for the mutualism between plants and mycorrhizal fungi but also for other types of mutualisms such as pollinators or seed dispersers. However, not all types of mutualisms will have the same impact on plant invasions (Richardson et al 2000, Traveset and Richardson 2014). For example, many plants may survive and reproduce in the absence of their seed dispersers (although some plant species require to pass through the gut of a seed disperser for the seed to germinate), while for many plants reproduction will be highly affected in the absence of pollinators, and most plants will not even survive without appropriate mycorrhizal fungi (with the exception of non-mycorrhizal and facultative mycorrhizal plants, which only represent ca. 15% of all land plants; Brundrett and Tedersoo 2018). Further research is needed to evaluate the relationship between plant invasiveness and dependence on pollinators and seed dispersers.

In conclusion we presented clear evidence challenging the hypothesis that species with higher invasiveness depend less on mutualisms. On the contrary, we found that species that are more invasive depend more on mutualisms. Our work highlights the importance of positive interactions (i.e. mutualisms) in explaining non-native species success and spread. This result may help explain the high prevalence of mutualists such as mycorrhizal fungi on land plants where ca. 92% of all plants are associated with mycorrhizal fungi (Brundrett and Tedersoo 2018). Relying highly on mutualisms for the colonization of new areas clearly has associated costs, but these costs seem to be overwhelmed by the benefits obtained.

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Figure legends

Fig. 1: a) Linear regression among mean effect size (+ SE) of ectomycorrhizal fungi (EMF) inoculation on seedling growth and species invasiveness (Z score) for 34 *Pinus* species. The higher the Z-score the more invasive is a species. Species with Z-scores below zero are expected to be non-invasive. b) Linear regression among mean effect size (+ SE) of ectomycorrhizal fungi (EMF) inoculation on seedling growth and seed mass for 34 *Pinus* species. The lower the seed mass the more invasive is a species. Each dot represents a different *Pinus* species.